

FOOD, FORAGING, AND TIMING OF BREEDING OF THE BLACK SWIFT IN CALIFORNIA

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ABSTRACT.—The nestling diet and breeding seasonality of the Black Swift (*Cypseloides niger*) were studied in southern California 1990–1992. The peak (40%) of egg laying was in mid-June and the peak of fledging (60%) was mid- to late August ($n = 87$ nests). Winged ants comprised 91% ($n = 1179$ prey items, 10 boluses) of nestling diet. Three main prey size classes were found: 6, 8, and 13 mm. Food bolus mass increased and number of trips per day to feed the nestlings decreased with nestling age. The parents made short and long foraging trips during early morning hours and long trips from early to late afternoon. Short trips were observed only during the first half of the nestling period. During the last half of the nestling period, parent swifts made a single foraging trip per day that lasted about 12 hrs. Perhaps the short foraging bouts are for feeding the young, whereas the long foraging bouts are not only for feeding the young but also for parental energy storage. The single foraging bout, during the mid- and late nestling period, might also serve to store fat for migration by the adults. Received 13 Feb. 1998; accepted 24 Oct. 1998.

The Black Swift (*Cypseloides niger*) is a member of the subfamily Cypseloidinae which consists of 12–13 species, most of which are tropical or subtropical in their breeding distribution. The Black Swift is found locally in the West Indies, Middle America, and north through much of western North America to southeastern Alaska (Bent 1940; AOU 1957, 1983). For a species with such a wide latitudinal distribution, quantitative data on diet and timing of breeding are rare. Most of what is known about the Black Swift is limited to breeding and distributional records (e.g., Vrooman 1901, 1905; Michael 1927; Dixon 1935; Knorr 1961; Foerster 1987; Foerster and Collins 1990; Stiles and Negret 1994). This reflects the difficulty of studying this species because of its aerial life style and its usually inaccessible nest sites. Here I present new information on diet and timing of breeding of this species.

The Black Swift is a summer breeding visitor to western North America, and like many migratory species there, has a restricted breeding season. Furthermore, it has a proportionately large egg, a single-egg clutch, is single brooded, and has a long incubation and nestling period (Marín 1997). These factors

should constrain variation in the timing of breeding of the Black Swift.

Swifts catch airborne insects and ballooning spiders (Lack and Owen 1955, Whitacre 1991). During the reproductive season, breeding cypseloidine swifts accumulate insects and arachnids in the back of the throat continuing into the esophagus and bind them with saliva to produce a sticky assortment of insects. This insect conglomerate or food bolus is produced exclusively to feed the nestling(s) and have never been reported outside the breeding season. Alive or dead these insects are complete, making them ideal for identifying and quantifying diets. Hespeneide (1975) pointed out that one difficulty in analyzing bird diets is knowing which is more important: the number or the size of food items. Some diet studies of New World swifts have addressed both parameters [e.g., Whitacre (1991)]; however, most have emphasized only one or they had small sample sizes (e.g., Collins and Landy 1968, Hespeneide 1975, Foerster 1987, Bull and Beckwith 1993, Marín and Stiles 1993). Other authors have considered only the number of prey items (e.g., Beebe 1949; Rathbun 1925; Rowley and Orr, 1962, 1965; Marín and Stiles 1992). One problem in quantifying swift diets is the source of prey samples, either stomach contents or food boluses. Stomach contents of adults are prey items that the adult bird has fed upon, whereas food boluses are prey fed to nestlings. Thus, examination of stomach contents versus food boluses might produce different results. Because my focus

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was on the diet of Black Swift nestlings, I analyzed only food boluses.

METHODS

Most data were gathered during a study of the breeding biology of the Black Swift in the San Jacinto Mountains, Riverside Co., California. The study site is at 1500 m elevation, and the surrounding area is montane forest. The study site was visited 40 times from 1990 to 1992, between the months of May and September. Observations were made in blocks of 4 to 7 hours, from 05:00 to 12:00, 12:00 to 19:00, or 19:00 to 23:00 PST, throughout the breeding season. For more detailed information on the study site and distribution of visits see Marín (1997) and references therein.

Data on nestling diet were obtained from regurgitated food boluses from adult swifts captured upon arrival at the nest. The boluses were weighed immediately (to nearest 0.1 g; Pesola scale) and placed in a vial containing alcohol. Insects in the boluses were counted and measured to the nearest 0.1 millimeter with a micrometer under a microscope in the lab.

Ten boluses ($n = 1179$ prey items) were collected from different adults on different dates and years throughout the study to minimize nest disturbance. Seven boluses were collected in 1991 and three during 1992. Bolus mass and time of collection were recorded for nine of them. I measured the length of 15 randomly selected individual prey items per prey species per bolus, and I used the average length as the mean of that species in the specific food bolus. Insects were sorted to morphospecies and identified to families using Borror and DeLong (1970), Borror and White (1970), and Powell and Hogue (1979).

To assess timing of breeding, I combined field nest data ($n = 20$) with archived nest and egg data cards ($n = 67$; see Acknowledgments for list of sources), along with museum study skins and the literature. To determine length of the breeding season, I used egg laying, hatching, and fledgling periods. I restricted analyses of museum egg data cards to two areas in California: mountains (San Jacinto area) and coast (Santa Cruz Co.). I compared the estimated hatching date from the museum egg data cards to my own field data on hatching dates gathered at San Jacinto to look for potential date discrepancies between actual and estimated data. The incubation stage given in the egg data cards (e.g., fresh, commenced, advanced, etc.) was extrapolated using the known days of the incubation stage from San Jacinto (24 days; Marín 1997). I candled 16 eggs at San Jacinto and determined that no egg of this species could be blown without significantly damaging or destroying the shell by day 16–18. Thus, any museum egg specimen of this species was unlikely to have been collected beyond 18 days of incubation. I estimated the duration of each stage visible through candling as: “fresh” (0–4, 5 days) “veins and small embryo” (5–10 days), “embryo” (11–14 days), and “large embryo” (>15 days). These data were used

TABLE 1. Contents of food boluses ($n = 10$) of *Cypseloides niger* from San Jacinto, California.

Order	Family	Number
Isoptera		1
	Hodotermitidae	1
Hemiptera		27
	Pentatomidae	3
	Coreidae	10
	Miridae	2
	Reduviidae	11
	Nabidae	1
Homoptera		54
	Cicadidae	17
	Cicadellidae	36
	Aphidae	1
Neuroptera		8
	Hemerobiidae	1
	Myrmeleonitidae	3
	Corydalidae	1
	Family?	3
Coleoptera		1
	Buprestidae	1
Lepidoptera		3
	Pyralidae	1
	Family?	2
Diptera		11
	Family?	11
Hymenoptera		1074
	Formicidae	1074
Arachnidea		1
TOTAL		1179

to infer incubation stage (from the data cards) and to estimate egg laying dates. Using the known incubation and fledgling period (24 and 48 days, respectively; Marín 1997), the estimated laying, hatching, and fledgling dates were compared and then combined with field data. The dates were separated by month, and each month was subdivided into early, middle, and late.

Rainfall data were gathered for each month for the years of study (1990–1992) and also 1963–1973 from the Idyllwild Fire Department weather station about 1.5 km from study area (National Oceanic and Atmospheric Administration 1991, 1992).

I was able to identify adults individually because they were already banded by C. Collins and K. Foerster because this was the main study site that Foerster (1987) used for his MS thesis work.

RESULTS

Nestling diet and foraging.—All boluses were composed of one predominant prey species, suggesting that the birds had fed on swarming species or highly localized prey. Winged ants were the majority of prey items (91%; Table 1). In 10 boluses the average proportion of female winged ants was 79.5 %

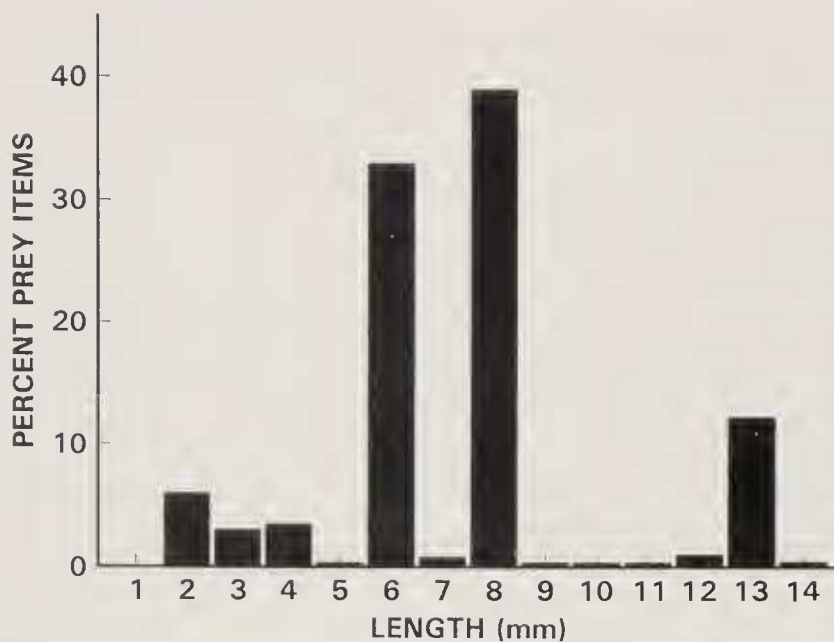


FIG. 1. Frequency distribution of prey sizes taken by the Black Swift (*Cypseloides niger*) in southern California. Data are from 10 food boluses ($n = 1154$ prey items); prey size categories are: 0.5–1.5 mm = 1; 1.6–2.5 mm = 2; 2.6–3.5 mm = 3; etc.

(range 20–100%; $n = 1179$ prey items). Sexual dimorphism in ants accounted for prey size differences among boluses. Male ants were smaller and ranged 2–6 mm, whereas females ranged 6–14 mm. Sometimes a bolus contained a small number of female ants but those ants were the largest prey. Thus, female winged ants had the highest volume/prey in all boluses. The average measurable prey size was 7.4 mm (range 1.8–14.5 mm; $n = 1154$). Three main size classes were found in the boluses: 6 mm (33%), 8 mm (39%), and 13 mm

(12.2%; Fig. 1). Two length categories (6 and 8 mm) made up the bulk of the samples. Because only a few prey taxa were represented in the diet, size frequencies for all prey species follow a similar pattern.

Nestling age and bolus mass were positively correlated ($r^2 = 0.93$, $P < 0.001$, $n = 10$; Fig. 2). No correlation was found between mean prey size per bolus and chick age ($r^2 = 0.08$, $P > 0.05$) or mass per bolus ($r^2 = 0.04$, $P > 0.05$, $n = 10$). No individual prey item was weighed, but female winged ants were

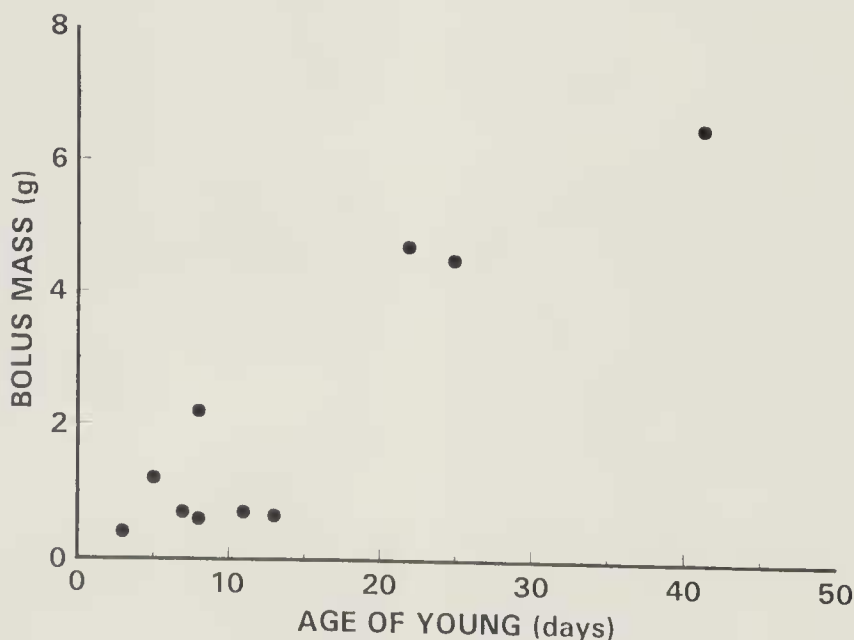


FIG. 2. Relationship between bolus mass and nestling age ($r^2 = 0.93$; $P < 0.001$, $n = 10$).

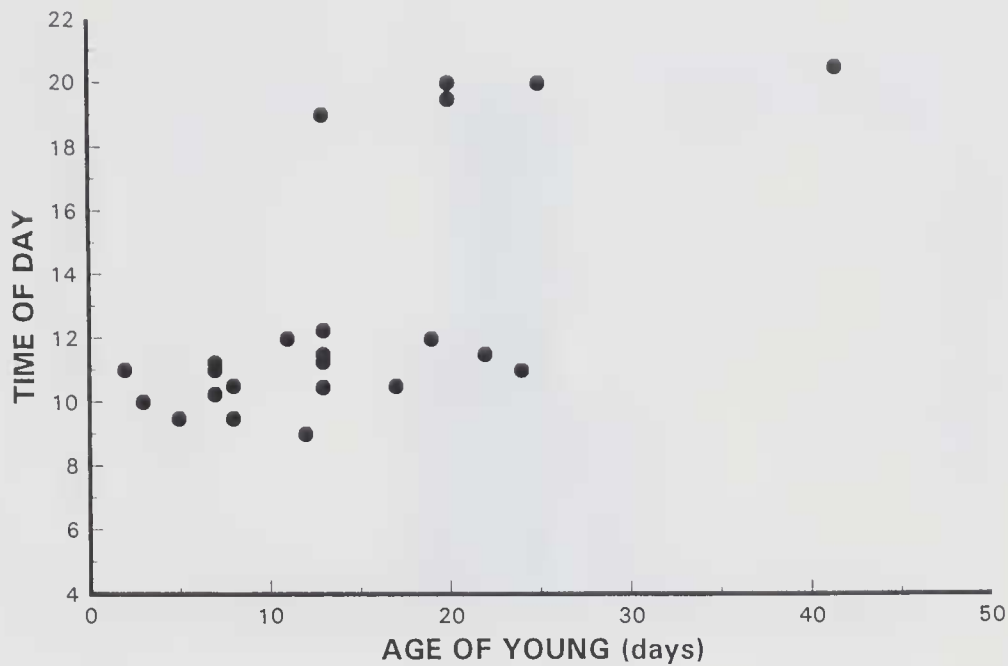


FIG. 3. Time of day young were fed versus their age. None of the adult birds were observed feeding young between the two feeding clusters or during early morning after 30 days.

undoubtedly the heaviest prey items because they were the largest. After day 30 I never saw any adults feed young in the morning; they were fed mainly late in the evening (Fig. 3). Other nestlings not included in the analysis because they were inaccessible and of unknown age, but at least 30 days old, were also observed being fed between 18:30–20:00. The overall pattern seems to be that as age increased, feeding rate decreased, but bolus mass increased (Figs. 2, 3).

Data gathered from adults feeding young at the nest showed two clusters of feeding times: between 8:30 and 12:30 and after 18:30 (Fig. 3). The birds usually left the cave at about 05:30. In two instances, however, some departed earlier unnoticed because of the darkness. This implies that they spent 3–7 hours searching for food for the first feeding bout. For the second bout, the birds were away from the nest longer: 6–8 hrs (Fig. 3). I never observed nestlings being fed between 12:30–18:30. I did not gather data late in the evening or at night during the early nestling stage so late arrivals and feeding at that stage are possible. If the intervals between feeding bouts were consistent through the season, then older nestlings often waited more than 12 hrs between meals when they were well grown or more than 30 days of age.

Breeding season.—Hatching dates were the

main variable I used to compare the timing of breeding between a mountain site (San Jacinto area, San Bernardino Co., California) and a coastal site (Santa Cruz area, Santa Cruz Co., California). The San Jacinto data were primarily from my observations, whereas the Santa Cruz data were taken from museum nest and egg data cards. I found no significant difference between the coastal and mountain sites in timing of hatching (Fisher's exact Test (2-tail): $P > 0.05$). Therefore, I concluded that it was safe to pool both field and museum data for coastal and interior southern California. Most eggs were laid during mid-June (40%), with 30% during late June (Fig. 4). The earliest laying date was estimated to be 18 May, from an egg set collected in 1960 near Santa Cruz, California. The latest date for egg laying on the data cards was estimated to be 12 July 1921, from the same site as the earliest date. Some of the observed variation might be due to inter-year differences, which are difficult to evaluate with the present data. Nevertheless, most eggs (81%) had an estimated laying date in June. The earliest estimated date for hatching was about 11 June (same nest as above) and the latest date was about 5 August from the same site. In total, 89% of the hatching dates were in July; 24% of the estimated hatching dates were during the first 10 days of July and 53% during the middle third of

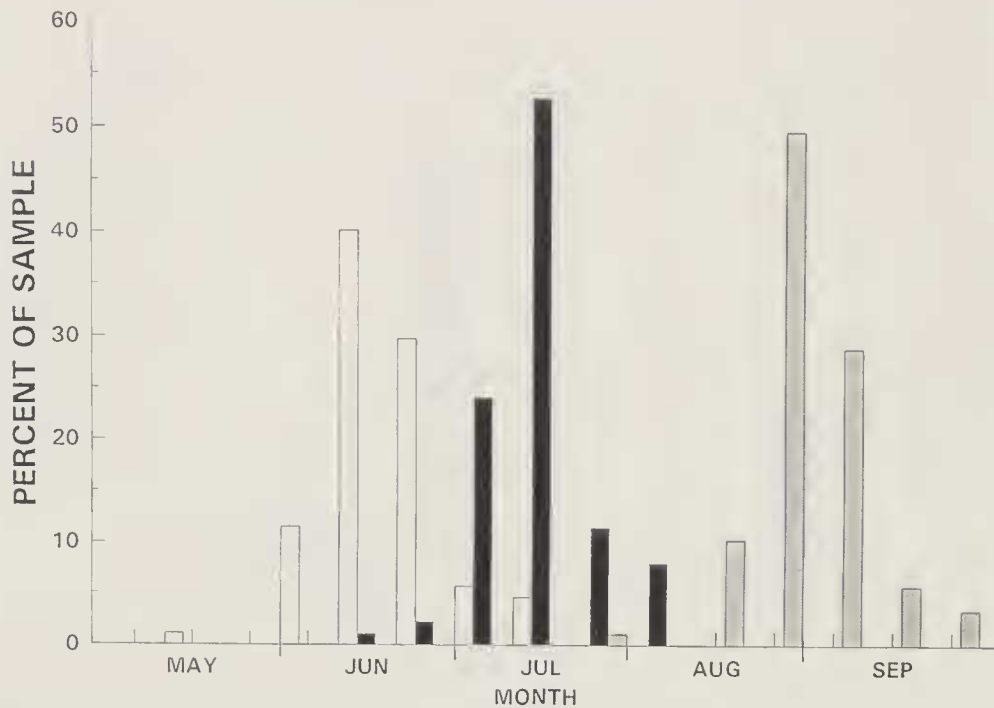


FIG. 4. Distribution of estimated dates of egg laying (open bars), hatching (black bars), and fledging (stipled on bars) of Black Swifts in southern California.

July. Sixty percent of the young were estimated to fledge during mid- to late August and 29% during the first 10 days of September. The highest proportion of fledging (78%) was estimated to occur between late August and early September (Fig. 4).

DISCUSSION

Contrary to most, if not all tropical cypseloidines, the southern California populations of the Black Swift breeds during the dry season. For the small, tropical cypseloidine swifts, rainfall itself can be as important a stimulus as food in initiating breeding. Moisture is needed to keep the appropriate conditions for nest "growth" and maintenance (Marín and Stiles 1992). Many Black Swifts did not build a nest at all, instead laid eggs directly on ledges, especially in the coastal sites (Marín 1997). This might be related to the lack of the proper nesting materials (mosses and liverworts).

The breeding season of the Black Swift in southern California is spread over 4.5–5 months (Foerster 1987, Marín 1997). Lack (1954, 1968) observed that breeding in most species of birds is timed to occur when food is most abundant, especially in temperate regions.

In the western United States, Chapman (1954) noted that ants swarmed from May

through September and that the peak of ant swarming was July. The observed peak of egg hatching in Black Swifts was also July coinciding with the peak of ant swarming (Fig. 5). These data support Holroyd's and Jalkotzy's (*in* Campbell et al. 1990) suggestion that the breeding of the Black Swift in southwestern Canada was timed to the swarming of flying ants (Hymenoptera). In the western U.S. ants swarm in large numbers on mountain and ridge tops for several days (Chapman 1954). The peak time of ant swarming observed by Chapman (1954) was from 07:00 to 14:00 and coincides with the first period of shorter feeding bouts in the Black Swifts (Fig. 3).

Foerster (1987) reported average prey sizes from two boluses ($n = 289$ prey items) as 9.9 and 10.2 mm, slightly larger than my averages. He did not report sizes smaller than 7 mm or larger than 13 mm. Foster (1987) speculated on possible size selection by the swifts; however, I observed 46.5% percent of prey items below and above those categories ($n = 1179$ prey items, 10 boluses). The data from this and other studies (Collins and Landy 1968, Foerster 1987) suggest that prey items given to the nestlings are selected not by size but by insect taxon. This is probably a consequence of feeding on insect swarms.

The main diet of Black Swift nestlings at San Jacinto was winged ants, which have a

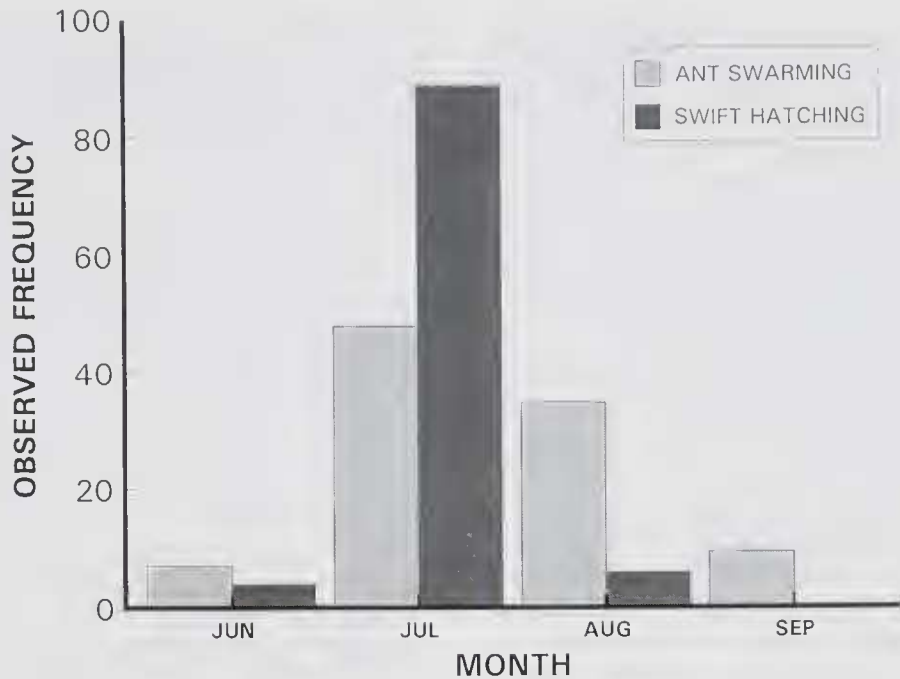


FIG. 5. Frequency of Black Swift hatching and ant swarming in southern California. Data for ant swarming are from Chapman (1954).

high fat content. The large preponderance of winged ants in the nestling diet is similar that of other cypseloidine swifts (Whitacre 1991). The percent fat per dry weight in alate ants ranges from 23.8 to 59.5% in females and from 3.3 to 9.6% in males (Taylor 1975, Redford and Dorea 1984). A nestling of any bird species fed a diet rich in energy could accumulate large amounts of subcutaneous fat. Before fledging the young Black Swift accumulates much visible subcutaneous fat and attains up to 148% of adult body mass; it reaches adult mass at day 15–16 of the nestling period (Marín 1997). The limited inter-year sampling by Foerster (1987) and myself suggests that the swifts at San Jacinto, during the breeding season, may specialize in exploiting local concentrations of 2–3 ant species (*Camponotus* spp.). Winged ants are a temporarily superabundant, patchy, and ephemeral, but lipid-rich food source. Other important prey items included Hemiptera and Homoptera (Table 1).

From scattered observations, (e.g., Michael 1927, Smith 1928, Bent 1940, Collins 1998, Collins and Peterson 1998) there is a general agreement that Black Swift nestlings are fed at long intervals, primarily early in the morning and late in the afternoon or at night. My data corroborate those conclusions (Fig. 3). The alternation of long and short foraging

trips resembles the strategy of energy expenditure described for foraging and food delivery in pelagic seabirds. Charurand and Weimerskirch (1994) and Weimerskirch and co-workers (1994) showed that long trips were primarily for parental food storage as well as nestling food gathering, whereas short trips were used to deliver food to the nestlings. Although the duration of seabirds' trips is days, instead of hours as in swifts, they might well serve analogous purposes.

Like seabirds, the Black Swift might gain weight on the long trips and lose it overnight. Black Swifts have a high metabolic rate and lose on average 7.9 % of body mass overnight (Marín, unpubl. data). Thus, the need for the long foraging bout is in accordance with the energy storage hypothesis (Chaurand and Weimerskirch 1994, Weimerskirch et al. 1994). Black Swift migration occurs immediately after the nestlings fledge; other species of swifts (e.g., *Chaetura* spp.) stay a few months after breeding, probably to store some energy for migration (Marín 1997). Accordingly, this long single foraging bout might also serve to store energy for migration, particularly during the later part of the breeding season.

As the Black Swift nestlings increase in age, it seems that the adults feed them only late at night. Quantitative data on feeding

rates or number of trips per day with respect to nestling age are scarce; however, declines in the number of trips per day with nestling age have been reported in other swift species (Malacarne et al. 1992, Oniki et al. 1992).

Lack (1954, 1968) suggested that seabirds with long nestling periods and single egg clutches were energy limited. This energy limitation was in food finding, food delivery, or both. Some swifts, particularly cypseloidines, have life history parameters similar to procelariiform seabirds (Lack and Lack 1951; Lack 1956, 1968; Marín and Stiles 1992; Marín 1993). For example, the Black Swift rears a single, slowly growing nestling, which suggests a constraint in either finding or delivering food. Because Black Swift nestlings require a highly specialized diet in order to have an initial fast growth and acquire a size larger than the adult quickly. I predict that the major constraint is food finding.

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